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CAUSES AND CONSEQUENCES OF THE VARIABILITY OF LEAF LIFESPAN OF FERNS

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ABSTRACT

Leaf lifespan (LLS) is a fundamental ecological trait of special importance to growth and survival of ferns. The LLS of ferns varies between two and 49 months depending on species and site conditions. Whereas temperate ferns are mainly summergreen, tropical ferns are mostly evergreen. However, some tropical ferns have seasonal or even deciduous leaf phenologies or dimorphism with shorter-lived fertile leaves that are produced only during a specific time of the year. The median LLS of tropical ferns of 19.2 months is nearly twice as long as in seed plants (10.0 months). Possible correlates of leaf lifespan such as leaf mass per area, nutrient content and herbivore damage, and future research questions are discussed.

INTRODUCTION

Leaves are the most conspicuous parts of ferns, with the exception of tree ferns that also have trunks of up to 15 m height. Ferns have developed leaves of all sizes, from large 4-5 m long leaves (e.g. *Angiopteris evecta* (G. Forst.) Hoffm.) to the smallest leaves of 1-3 mm length of *Azolla filiculoides* Lam. and some species of filmy ferns such as *Didymoglossum ovale* E. Fourn.

Because of the importance of leaves as "energy transformers", their number, size and functional characteristics such as lifespan are of special importance to growth and survival of plants. Whereas the number of leaves, their size and other morphological traits can be easily measured at any time, the direct measurement of leaf lifespan (LLS) requires their entire ontogeny to be followed from the first appearance of a developing crozier through expansion, maturation and death (though not necessarily detachment). Some authors measure the LLS as the time from the moment the leaf is fully expanded to leaf death (Kikuzawa & Lechowicz, 2011), a definition which would result in estimates of LLS which are from two to eight weeks shorter because of the time needed for the crozier to complete leaf expansion. Leaf lifespan can also be estimated by dividing the mean leaf number by the annual leaf production (see Mehltreter, 2008). Both direct measurement and estimation require several observations throughout at least one year and consequently few data are available on fern LLS. For example, Wright *et al.* (2004) included 13 fern species in a dataset of 2548 vascular plant species, but only two of those fern species contained data on LLS. For the current review, we compiled a dataset of 71 fern species, which is still less than one percent of the currently known 9500 fern species (excl. lycophytes, Smith, 2010).

The LLS of ferns varies in temperate climates as well as in tropical climates, and species of different LLS may coexist at the same sites (Shiodera *et al.* 2010). Consequently, we asked:

How much does LLS vary in ferns? Does mean LLS differ between ferns and angiosperms? How does LLS vary between species, sites and within the geographic range of a single species? Which leaf traits are correlated with LLS?

VARIATION IN FERN LEAF LIFESPANS

Leaves of the shortest lifespan may belong to some species of grape ferns (*Botrychium)*, which may persist for 1.8 months (*B. gallicomontanum* Farrar & Johnson-Groh) to 2.8 months (*B. mormo* W.H. Wagner) in Minnesota, U.S.A. (Johnson-Groh & Lee, 2002), whereas the longest mean LLS of 4.9 years was reported for fertile leaves of *Terpsichore asplenifolia* (L.) A.R. Sm. (Monge Gonzalez, 2007), a Mexican epiphyte with overhanging leaves of indeterminate growth. Leaves of indeterminate growth have a very long potential LLS, supposedly unlimited by intrinsic factors (e.g. plant hormones), but die mainly as a consequence of abiotic factors (e.g., lack of water, mechanical damage) or biotic interactions (e.g., herbivores, fungal infections). Leaves of smaller, younger plants of *T. asplenifolia* are still of determinate growth, remain sterile and are shorter lived than the fertile leaves of larger plants. As a consequence of their indeterminate growth, leaves of *T. asplenifolia* are capable of continuous spore production because they possess all stages of sporangia, old sporangia which already have released their spores near the leaf base, fully developed sporangia with mature spores in the mid-section of the leaf and immature new sporangia near the leaf tip.

The LLS can differ considerably for species that occur over a wide geographical range. *Botrychium virginianum* (L.) Sw. occurs from Canada to Peru under distinct climatic conditions and growth seasons of different duration. In North America, leaves of *B. virginianum* appear in early spring and die in late summer, a period of about four months (Wagner & Wagner, 1993). However, in Mexico the LLS of *B. virginianum* is 17.1 months, and thus a new leaf may coexist for several months together with the leaf of the year before. On the other hand, *Acrostichum danaeifolium* Langsd. & Fisch., one of the few species that has been studied at different sites, maintained a similar LLS in Mexico (7.7. months; Mehltreter & Palacios-Rios, 2003) and Puerto Rico (9.6 months; Sharpe, 2010).

The median LLS for our dataset of 71 fern species was 15.6 months (range 1.8-48.9 months), much longer than the median LLS of 8.5 months for seed plants (range 1.1-288 months, Wright *et al.,* 2004). However, it is difficult to assess the validity of such a comparison because it could be biased by factors such as species selection, disturbance regimes, phylogenetic constraints, or geographic location. In our dataset, 91.5% of fern species came from tropical areas, where we expect LLS to be longer. Restricting the analysis to tropical species, the median LLS for ferns, 19.2 months (first quartile = 11 months, third quartile = 24.6 months, n = 66), is still significantly longer than that for angiosperms, 10.0 months (first quartile = 7.0 months, third quartile = 19.1 months, n = 163, Mann-Whitney $U = 3633$, $P < 0.001$). No significant differences of LLS among four of the five tropical fern floras could be detected, but ferns of Puerto Rico had a significantly longer LLS than ferns of Hawaii and Mexico ($F = 3.71$, $P = 0.009$, Table 1). Further studies are needed to determine whether these differences are consequence of the selection of sampled species we used or if they represent a real contrast among fern floras.

Table 1: Sterile LLS of ferns (in months) at different tropical sites, S.E. = Standard error

Site	Mean LLS ± 1 S.E.	Minimum LLS	Maximum LLS
Hawaii (n = 14)	15.0 ± 1.75	5.0	24.6
Jamaica (n = 3)	17.3 ± 3.76	11.0	24.0
Puerto Rico (n = 14)	26.5 ± 3.44	8.4	48.9
Mexico (n = 17)	16.4 ± 1.89	5.5	32.0
Taiwan (n = 18)	17.5 ± 1.82	5.1	30.3

TEMPERATE FERNS

There are three general LLS categories for temperate ferns: summergreen, wintergreen and evergreen. Summergreen ferns produce a flush of new leaves in spring (e.g. *Adiantum pedatum* L., *Matteuccia struthiopteris* (L.) Tod.) that die at the end of the summer growing season. In contrast, wintergreen species retain some green leaves through the winter until the following spring or summer, just before or after a new set of leaves begins to develop. The leaves of evergreen ferns are not produced in a seasonal flush, but are replaced as older leaves die and consequently the plants are never leafless. Although leaves of most evergreen species live for more than a year, LLS may still differ considerably among species.

Phenograms for much of the temperate fern flora of Britain and Ireland have been published (Page 1997) and from them we estimated LLS by counting the months from leaf maturity (ignoring expansion phase) to full senescence. Using terminology defined by Lellinger (2002) we then classified the taxa in this flora as 27 summergreen, 9 wintergreen and 11 evergreen species with mean LLS of approximately five, 11 and 16 months, respectively. In the British flora, LLS varies between four months (*Botrychium lunaria* (L.) Sw.) and 25 months (*Polystichum lonchitis* (L.) Roth). Combining the 13 phenological types identified by Sato & Sakai (1980) for mature leaves into the same three categories of Lellinger (2002) results in a temperate fern flora for Hokkaido, Japan that has 42 summergreen, 11 wintergreen and 15 evergreen species, with the high ratio of summergreen to evergreen species at high latitudes contrasting with a very low ratio at lower latitudes in Japan. Sato (1982) further documents the correspondence between frost tolerance and LLS category, with few frost tolerant leaves found among the summergreen species. In the flora of one area of Japan (Yoshida & Takasu, 1993) mean LLS of 21 species ranges from five months (*Deparia pycnosora* var. *alvosquamata* M. Kato) to 37 months (*Asplenium wrightii* D.C. Eaton ex Hook.).

Whereas summergreen ferns store all their nutrients and energy in the rhizome or roots during the winter and then reinvest in new leaves during the following season, wintergreen and evergreen species expose their leaves to cold temperatures and even

frost, but still benefit from photosynthetic gains during mild winter days (e.g., *Dryopteris filix-mas* (L.) Schott; Bauer *et al.,* 1991). Because longer living leaves of wintergreen and evergreen ferns have to survive a wider variation of environmental conditions than shorter-lived leaves of summergreen ferns, their longer LLS are often correlated with robust leaf structure and greater leaf mass per area (LMA, see below).

TROPICAL FERNS

Ferns of tropical habitats are often evergreen due to the lack of seasonality in temperature and rainfall. However ferns in tropical as well as subtropical areas that undergo dry seasons of several months may be deciduous because drought may cause stress to the leaves resulting in leaf drop patterns similar to those caused by cold temperatures in temperate areas. Some epiphytic fern species are also deciduous and sprout new leaves at the beginning of the rainy season (e.g., *Phlebodium areolatum* (Humb. & Bonpl. ex Willd.) J. Sm., *Polypodium rhodopleuron* Kunze). Such epiphytes may be even more exposed to water stress because they are rooted in shallower substrate than terrestrial ferns. Other species, such as the Mexican tree fern *Alsophila firma* (Baker) D.S. Conant which grows in the understory of montane forests, are not exposed to severe drought stress at their natural sites (Mehltreter & García-Franco 2008). However shorter LLS (Chabot and Hicks, 1982) and deciduousness followed by synchronous leaf flush have been reported to reduce herbivore damage (Lieberman & Lieberman, 1984; Karban, 2007). Consequently, *A. firma* might be deciduous during the wet season when herbivorous insects thrive and develop all new leaves synchronously two to three months after leaf fall. Water is never scarce in mangrove forests but plants have to deal with increased salinity of soil water. The mangrove fern *Acrostichum danaeifolium* Langsd. & Fisch does not possess any specific mechanism for eliminating sodium such as the salt glands of other mangrove species. Consequently, sodium is accumulated in the leaves and is eliminated only when leaves die, perhaps accounting for the LLS of 7-10 months, relatively short for a tropical fern (Mehltreter & Palacios-Rios 2003, Sharpe 2010). Indeterminate leaves of climbing ferns such as *Lygodium venustum* Sw. suffer from disturbances such as branch falls and their measured LLS of 5.6 months might be far below their potential LLS without external disturbance factors (Mehltreter 2006).

POSSIBLE CORRELATES OF LEAF LIFESPAN

In the following, we discuss several general hypotheses that have been suggested as correlations between LLS and other plant characteristics. These hypotheses are often based on knowledge of angiosperms, and we relate it to our dataset of ferns.

A longer LLS increases the time available for photosynthetic gains, but requires more structural investment to resist unfavorable environmental conditions such as frost or drought. According to this hypothesis, evergreen leaves have a higher leaf mass per area (LMA) than deciduous leaves (see Kikuzawa and Lechowicz, 2011). For eight fern species of our data set for which LLS and LMA are available, this correlation is significant (Pearson correlation coefficient $r = 0.75$, $P = 0.03$, Figure. 1a). In addition, LMA is negatively correlated with nitrogen (N) content ($r = -0.81$, $P = 0.01$).

Greater environmental tolerance of longer-lived leaves has a tradeoff resulting in lower photosynthetic rates and lower N concentrations. Available data for ferns are not significant (both $P = 0.11$, Figure 1b and 1c). Most ferns have generally lower photosynthetic rates than angiosperms (see Mehltreter, 2010), supposedly because of their lower water transport efficiency and lesser control of water transpiration (Orians &

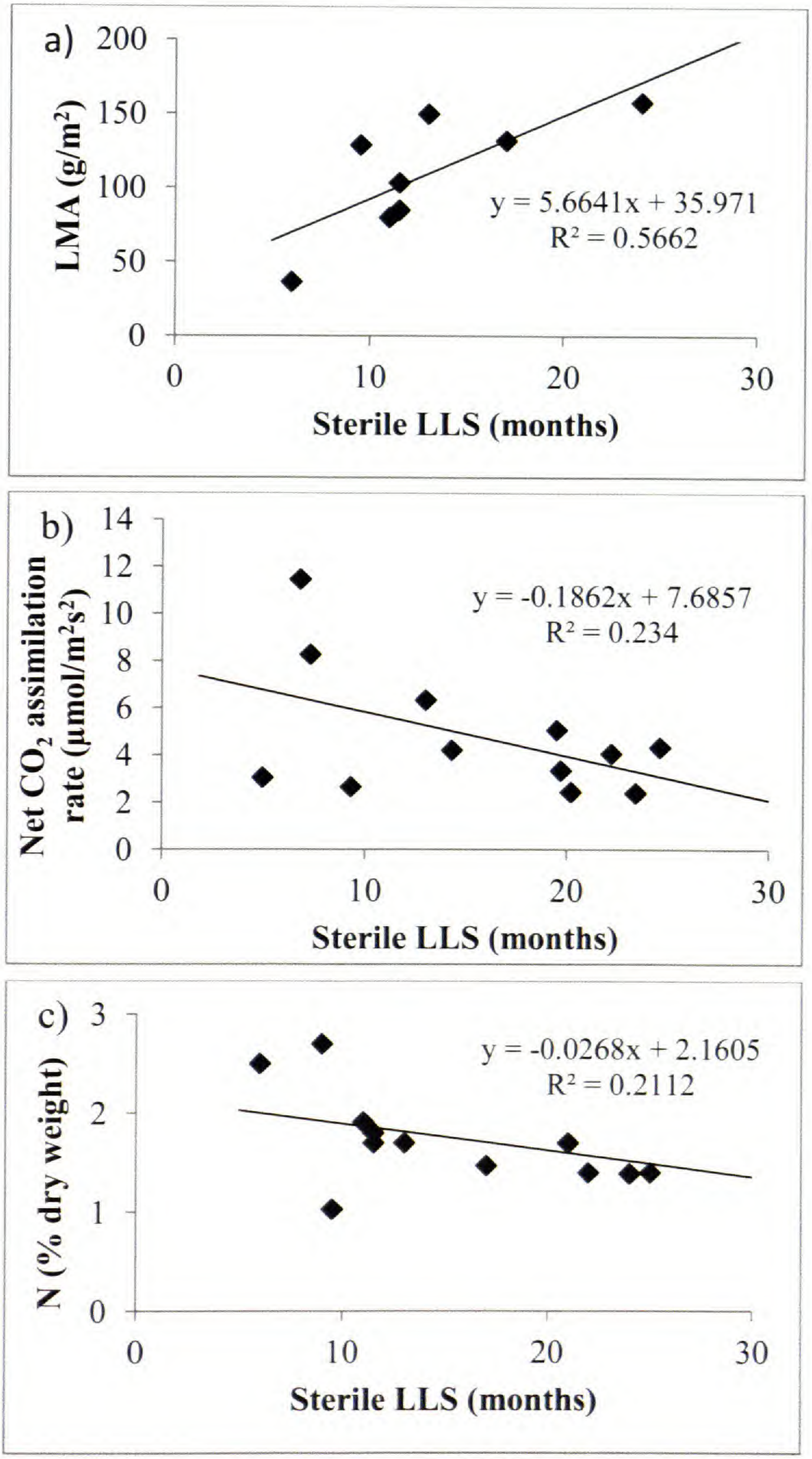

Figure 1. Correlation between sterile LLS and a) LMA b) Net CO_2-assimilation rate and c) N content in tropical ferns. Data from Baruch & Goldstein 1999[ac], Chiu *et al.* 2013[b], Durand & Goldstein 2001[ac], Funk & Amatangelo 2013[b], Tanner 1983[ac], Winkler *et al.* 2005[c].

Solbrig, 1977; Brodribb *et al.*, 2005).

A longer LLS should increase nutrient retention and recycling. Richardson *et al.* (2010) found that angiosperm species on nutrient-poor sites did not exhibit an increase of LLS but rather did exhibit an increase of nutrient resorption efficiency, so that new leaves receive part of their nutrients from older, dying leaves. Longer LLS has been related with lower N content, higher silicium (Si) content (Cooke & Leishman 2011) and perhaps also higher aluminum (Al) content in some tropical angiosperm species. Data for ferns are limited, but Tessier & Bornn (2007) found that overwintering leaves of *Dryopteris intermedia* (Muhl. ex Willd.) A. Gray provide a carbon source for new leaves but not a nitrogen source, findings similar to those of Tani & Kudo (2003) in *D. crassirhizoma* Nakai.

A longer LLS makes leaves of fern species more vulnerable to herbivore damage. Such damage will increase during the lifespan of the leaf, and thus slow growing species may not be able to produce enough new leaves to compensate for the lost leaf tissue. As a consequence, it was suggested that species with a longer LLS may invest more in secondary biochemical defense mechanisms against herbivores (Chabot & Hicks, 1982; Coley, 1980). For ferns of nutrient poor and dry environments herbivore damage is even more problematic, because the replacement of lost leaves requires considerable investment of sparse resources. At a study site in Mexico, epiphytic ferns indeed had a longer mean LLS than terrestrial species but similar levels of leaf damage (Mehltreter *et al.*, 2006). For xerophytic and epipetric species no data are available.

In fern species that exhibit sterile-fertile leaf dimorphism, fertile LLS is shorter than sterile LLS. In several fern lineages, species with dimorphic leaves (e.g. *Blechnum*, *Bolbitis*, *Plagiogyria*) also exhibit marked differences in LLS. The lowest ratios of fertile/sterile LLS have been reported for species of *Danaea* from Puerto Rico (10-25%, Sharpe & Mehltreter 2010) and *Plagiogyria* from Taiwan (16-20%, Lee *et al.*, 2009), species which also have extreme morphological differences between the two leaf types. A similar effect can be seen in partly fertile leaves, where only apical, central or basal parts of the leaves produce sporangia. For example, *Acrostichum aureum* L., *Polystichum acrostichoides* (Michx.) Schott and *Belvisia mucronata* (Fée) Copel. produce sporangia at their apical leaflets and leaf tip, respectively, and these fertile leaf parts die after some weeks whereas the rest of the leaf stays alive for several more months. The interrupted fern, *Osmunda claytoniana* L. has its fertile leaflets in the central part of the leaf, and when they die there appears to be an interruption in the leaf lamina. Species of *Anemia* have modified their basal leaflet pair, developing into erect, fertile leaflets, which also die months before the horizontally expanded, sterile part of the leaf. In contrast, LLS is similar for species with monomorphic leaves, where leaf form and size are the same for sterile and fertile leaves (Figure 2). In some monomorphic fern species, however, fertile leaves can be longer lived than sterile leaves. For example, in *Cibotium taiwanense* C.M. Kuo the fertile leaves live 156% longer than sterile leaves, perhaps because in this species, it has been reported that fertile leaves shed the spores during the second year rather than immediately after leaf maturation (Chiou *et al.*, 2001).

Dead leaves of some fern species may still indirectly serve the plant. Some fern genera such as the epiphytic *Drynaria* and *Platycerium* produce heteromorphic leaves. Short-lived niche or shield leaves that function as humus accumulating structures contrast with longer lived, photosynthetic and sporangia bearing leaves. The niche leaves are green during development, but die early. However, even dead, their tough, shield-like lamina, pressed against the tree bark or building a pot-like structure together with other

dead leaves continue to function as humus accumulator. In other fern species, dead leaves possess such a rigid petiole and rachis that they still work as a protective shield for adjacent living leaves against wind, high irradiance or frost such as in the xerophytic species of *Cheilanthes* or the paramo fern genus *Jamesonia.* In the climbing fern genus *Lygodium*, the rachises of dead leaves are the main climbing structure for young leaves to reach the canopy (Mehltreter, 2006).

Fern species with faster growth rates have a shorter LLS. The faster growing fern species develop in sunny, open habitats and can produce more leaves in a year than shade tolerant species. Siman & Sheffield (2002) have shown in greenhouse experiments with *Polypodium vulgare* that leaf production rates increase with increased light and temperature. Leaves of sun species have shorter LLS than shade species, and sun leaves have a shorter LLS than shade leaves of the same individual (Reich *et al.*, 2004; Vincent, 2006). In Hawaii the introduced Australian tree fern *Sphaeropteris cooperi* (F. Muell.) R.M. Tryon has shorter LLS than the native, shade tolerant species of *Cibotium* (Durand & Goldstein, 2001). Because of its fast growth, *S. cooperi* invades and outcompetes the native Hawaiian tree ferns (Medeiros *et al.*, 1992; Chau *et al.*, 2013).

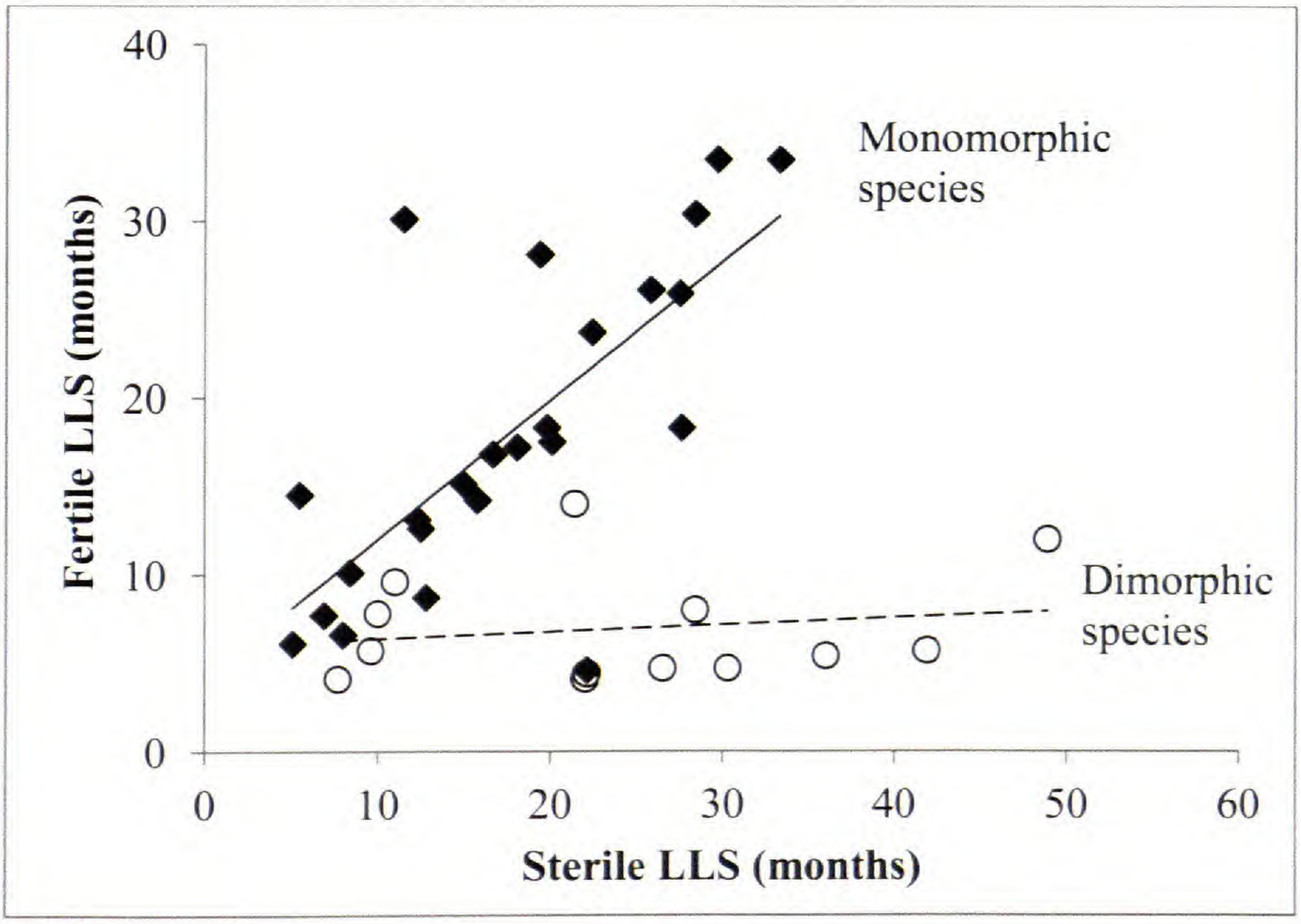

Figure 2. Leaf lifespan of monomorphic (filled diamonds) and dimorphic species (empty circles). In monomorphic species, sterile and fertile leaves have a similar lifespan, whereas in most dimorphic species fertile leaves are shorter lived. *Woodwardia semicordata* is an exceptional monomorphic species with long-lived sterile leaves (22.1 months) but relatively short-lived fertile leaves (4.6 months). Lines indicate linear regressions for monomorphic and dimorphic species.

CHALLENGES FOR THE FUTURE

We need to establish a larger and more consistent database of ecological life histories of ferns that includes, at a minimum, leaf characteristics such as LLS, LMA, nutrient content and photosynthetic rates and then to detect functional consequences of these traits to allow for more profound analyses of the role of ferns in an ecosystem. Some data on each of these characteristics exist, yet are scattered throughout the literature. For example, Watkins *et al.* (2010) took photosynthetic measurements on 21 species of tropical ferns but summarized the results by habitat and did not include LLS in their analyses. Karst & Lechowicz (2007) compare fern foliar traits with those of seed plants, and include LMA and photosynthetic rates but not LLS, and base their fern conclusions on the very limited data from Wright *et al.* (2004). Measurements of a single species over a wide geographic range could reveal the limits on adaptability of various leaf traits in changing environments. Experimental greenhouse studies could be used to investigate which factors such as nutrient concentrations may be correlated with longer LLS. Physiological experiments are also required to better understand which factors trigger the ontogenetic development into sterile or fertile leaves, especially in dimorphic fern species. Long-term studies over decades may allow the identification of responses to global climate change and should be established in protected sites such as those within the International Long Term Ecological Research network.

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BIOGRAPHY - JOANNE M. SHARPE

Joanne M. Sharpe is an independent Consultant specializing in fern ecology, long-term studies and the role of amateurs in ecological research. She lives in Maine but has been a Research Associate with the NSF-funded Luquillo Long-Term Ecological Research (LTER) Program in Puerto Rico for over twenty years. She is currently writing up the results of a several long-term studies fern growth and spore production as part of tropical forest (and mangrove) productivity, hurricane impact, and demographic projects. Joanne grew up in Michigan and New York and has a degree in English from the University of Houston (Texas), a masters in Regional Planning from the University of Massachusetts and a doctorate in Botany from the University of Georgia. After a career in computers, Joanne discovered tropical ferns in a ecological seminar at the Asa Wright Center in Trinidad and her fascination with the mysteries of their ecology led her to graduate school where she worked in Costa Rica and published four papers on the demography, tropic responses and vegetative reproduction of a forest floor fern, *Danaea wendlandii*. This was followed by publications of long-term studies of individually marked plants over 25 different species in Puerto Rico and two temperate ferns. She lectures at meetings ranging from the USA to the UK to India and Costa Rica in hopes of inspiring others to do more global studies of the demography of ferns. She spent 17 years maintaining the membership data base and producing the *Annual Review of Pteridological Research* for the International Association of Pteridologists. Joanne was also a co-editor of the book *Fern Ecology* and co-author of several of the book's chapters.

BIOGRAPHY - KLAUS MEHLTRETER

Klaus Mehltreter has been researcher and professor at the Department of Functional Ecology at the Instituto de Ecología, A. C. in Xalapa, Mexico since 1998. His research interests focus on fern ecology, especially the seasonality of growth and reproduction, their contribution to local biodiversity and ecological function in local plant communities, and their interactions with insects. He teaches tropical field courses on plant ecology, management of databases for research and scientific writing. He studied biology at the University of Ulm, Germany where he was research assistant from 1986-1996, and where he also received his doctorate of Natural Sciences in 1994. From 1997-1998, he worked as an independent researcher at the Commission of Scientific Research of the Province of Buenos Aires, Argentina to develop floristic databases. Since 2004 he has been a member of the National System of Researchers of Mexico. In 2009, he spent a sabbatical at the University of Hawaii to work on the ecological impact of invasive fern species. He is author of over 40 publications, has coauthored three books and edited the book *Fern Ecology*, together with Lawrence Walker and Joanne Sharpe. Currently, he is compiler of the Annual Review of Pteridological Research for the International Association of Pteridologists and serves as associate editor for the Fern Gazette and the American Fern Journal.

BOOK REVIEW

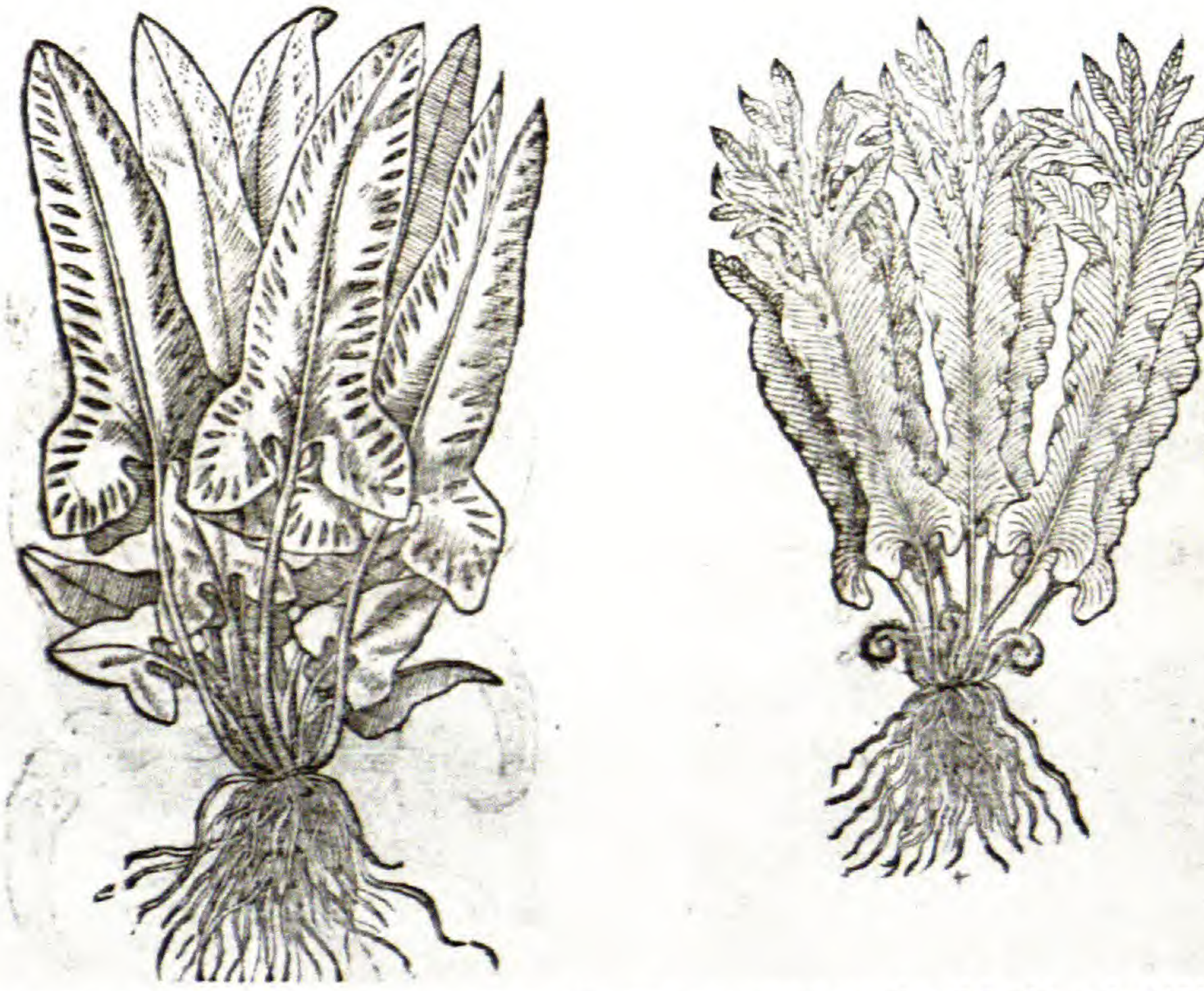
Who found our ferns? John Edgington. 2013. British Pteridological Society Special Publication No. 12 ISBN 978-0-9926120-1-6 216pp. £15. 245 x 170mm.

This meticulously compiled book has several different strands to document the history of discovery of each species of fern and Lycophyte recorded from Britain and Ireland.

The chapters are ordered using modern nomenclature and the species are shown subdivided by Classes, Orders and Families. A short account is given at the beginning of the chapter for each Family that includes any fossil evidence and a summary of the present knowledge of fern classification. Early identifications were of necessity based largely on gross morphology. By using molecular and chromosome information we now have access to many more resources than were available to the pioneer taxonomists, and the increase in species numbers within the flora in the twentieth century has resulted from recognition of species complexes in genera like *Polypodium* or *Dryopteris*. The author shows that relating current taxonomic concepts to early records can be quite a challenge.

The main part of the text chronicles a complicated search through many references and early herbarium records to unravel exactly which species is being described, sometimes from rather limited or inaccurate descriptions. An added complication in deciding which taxon was intended is that species which were abundant in the past might have a more restricted distribution now. The first record from each of the countries within Britain is given. The whole combines to provide a history of botanical recording and the developing understanding of plant classification for ferns and Lycophytes.

Before Linnaeus formalised the names of plants people used a descriptive Latin phrase which was considerably more cumbersome than the binomial names that evolved



Two varieties of *Asplenium scolopendrium*, treated as separate species (Matthieu de L'Obel, 1581)

into the names that are now use. Each chapter describes not simply a possible first record, but the first record that is unambiguously the taxon which we currently recognise by the stated name. In the midst of the confusion over early classification and multiple applications of the same plant names, one can sympathise with the difficulties and complications people encountered as they struggled to make sense of different species or varieties. In the search for early records of British species it was necessary to span across Europe to compare descriptions from the botanical community that were being applied within Britain. In interpreting the taxa it is sometimes necessary to go back to the names given to the plants in classical times that come to us as Greek or Latin words, some of which are still used as part of the scientific name. At the end of the book is a very useful summary of early names, synonyms and Latin phrase names showing how similar descriptive words have been used across so many species and even families that we now know were un-related.

Individual species accounts show the difficulties botanist encountered in attempting to describe structures that were not understood. Isoetes, for example, like many other species were first thought to be flowering plants strangely lacking both in flowers and seed. Further confusion was shown in the idea that the fertile cones of *Equisetum arvense* were a different species from the vegetative shoots. The situation improved with the understanding the of the fern life cycle in the late 18th century, but it was hardly surprising that *Pilularia globulifera* was not initially recognised as a fern.

It was interesting to find that the first recorded specimen of *Asplenium septentrionale* was from Holyrood Park in Edinburgh in 1669, where the ferns still thrive, despite Victorian predation. In a discussion of the crested variety of *Asplenium scolopendrium*, first mentioned in the 17th century, reference was omitted to a forked variety carved in the 15th century on the Apprentice Pillar in Rosslyn Chapel, but perhaps illustration alone does not qualify as publication.

Some species first recognised in this county during the Victorian fern collecting craze seemed to disappear almost as quickly as they were found, *Trichomanes speciosum* being a good example. There were others now known from very few herbarium specimens, such as *Cystopteris alpina*, possibly becoming extinct before they had been fully recognised. At least the species first found within Britain in the 19th century were better described and supported by herbarium specimens, but it is of note that more remote montane species such at *Athyrium distentifolium* and *Cystopteris montana* were only differentiated comparatively late. A recurring problem was the difficulty of determining whether morphologically distinctive taxa merited species or varietal rank. A major advance is acknowledged in Irene Manton's work on chromosome counts, published in 1950 and particularly useful in separating *Dryopteris* and *Polypodium* species and hybrids.

This is not merely an account of long-resolved taxonomic problems as controversies continue and new discoveries continue to appear. There is the *Trichomanes speciosum* gametophyte story that started in 1989 with the unexpected finding of gametophytes where the sporophytes had long since been lost. The gametophytes were subsequently found to be extraordinarily widespread, apparently very long-loved and remarkably resilient. *Cystopteris diaphana* was added to the British flora in 2000 and although our fern flora is comparatively small there is still scope for more discoveries.

This account is a detailed detective work through old records and specimens, and illuminates the excitement of discovery of our fern flora.

H.S. McHaffie

NEW COMBINATIONS AND LECTOTYPIFICATIONS FOR SOME SOUTH-EAST ASIAN, MALESIAN AND PACIFIC GRAMMITID FERNS (POLYPODIACEAE)

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Key Words: New combinations, lectotypifications, South East Asia, Malesia, Pacific, Grammitidaceae, Polypodiaceae

ABSTRACT

New combinations are made for *Ctenopterella nhatrangensis* (C.Chr. & Tardieu) Parris, *Oreogrammitis pubinervis* (Blume) Parris, *Oreogrammitis subevenosa* (Baker) Parris, *Prosaptia brassii* (Copel.) Parris, *Prosaptia javanica* (Copel.) Parris, *Prosaptia samoensis* (C.Chr.) Parris, *Stenogrammitis minutissima* (J.W.Moore) Parris, *Tomophyllum duriusculum* (Christ) Parris, *T. foersteri* (Rosenst.) Parris, *T. lividum* (Mett.) Parris, *T. secundum* (Ridl.) Parris and *T. sesquipinnatum* (Copel.) Parris. Lectotypes are chosen for *Polypodium emersonii* var. *samoense* C.Chr., *P. minutissimum* J.W.Moore, *P. secundum* Ridl., *P. subcoriaceum* Copel. & *P. subsecundodissectum* var. *novoguineense* Rosenst.

INTRODUCTION

Progress on revisions of grammitid ferns for Flora Malesiana and regional accounts in Southeast Asia and the Pacific necessitates the publication of the following new combinations.

NEW COMBINATIONS

1. Ctenopterella nhatrangensis (*C.Chr. & Tardieu*) *Parris* **comb. nov.**

Based on *Ctenopteris nhatrangensis* C.Chr. & Tardieu, Not. Syst. (Paris) 8(4): 181 (1939). Type: Vietnam, Nhatrang, Song Ko, 700 m alt., 18 May 1922, *Poilane* 3338 (BM 001039878!).

RANGE. Vietnam; endemic.

2. Oreogrammitis pubinervis *(Blume) Parris* **comb. nov.**

Based on *Grammitis pubinervis* Blume, Enum. Pl. Javae: 116 (1828). Type: Java [*Blume* s. n.] (lectotype L!, chosen by Parris, 2007). **Synonym**: *Polypodium pubinerve* (Blume) Christ, Ann. Jard. Buitenzorg 15: 146 (1897).

Oreogrammitis pubinervis has previous been regarded as a synonym of *O. setosa* (Parris, 2007), but differs from the latter in having the lamina glabrous on both surfaces.

3. Oreogrammitis subevenosa *(Baker) Parris* **comb. nov.**

Based on *Polypodium subevenosum* Baker in Hook. & Baker, Syn. Fil.: 320 (1867). Type: Penang, *Mactier* s. n. (holotype K!; isotypes E 00195211!, E 00195212!). **Synonyms:** *Grammitis subevenosa* (Baker) C.Chr. & Tardieu, Notul. Syst. (Paris) 8: 179 (1939). *P. sessilifolium* Hook., Sp. Filic. 4: 168 (1863) *non* Liebm. (1849). *G. sessilifolia* J.Sm., Hist. Filic.: 181 (1875) *nomen novum pro P. sessilifolium* Hook. (1863) *non* Liebm. (1849). *P. malaicum* Alderw., Malayan Ferns: 577 (1909), *nomen novum pro P.*

sessilifolium Hook. (1863) *non* Liebm. (1849). *G. malaica* (Alderw.) Tagawa, Acta Phytotax. Geobot. 8: 173 (1939), *nomen superfl. illegit. pro G. sessilifolia* J.Sm. *P. maxwellii* Baker, Bull. Misc. Inform., Kew 1893: 211 (1893). *G. maxwellii* (Baker) Parris, Fern Gaz. 12(2): 118 (1980).

RANGE. Thailand?, Vietnam, Peninsular Malaysia (Perak, Penang, Kelantan, Negeri Sembilan, Terengganu, Pahang, Melaka, Johor), Borneo (Kalimantan, Sarawak), Philippines (Palawan, Sibuyan), Moluccas (Seram), New Guinea (West Papua).

Oreogrammitis adspersa (Blume) Parris has only been collected once in Thailand according to Tagawa & Iwatsuki (1989, as *Grammitis adspersa*); perhaps the specimen belongs to *O. subevenosa,* as does all Peninsular Malaysian material examined.

Oreogrammitis subevenosa was previously regarded as a synonym of *O. adspersa* (Copeland 1952, Parris 1983, 2007, 2010), but differs from it in having glabrous rather than setose sporangia. *Oreogrammitis nuda* (Tagawa) Parris of Taiwan also has glabrous sporangia, but differs from *O. subevenosa* in having elongate, rather than ± circular, sorus receptacles. The receptacles are prominent on the adaxial surface of the lamina in both species. *Oreogrammitis nuda* and *O. subevenosa* always have a white deposit (sometimes hard to see) on the hydathodes of the veins on the adaxial surface of the lamina; some material of *O. adspersa* also has a white deposit on the hydathodes, but it is not characteristic of the species.

4. Prosaptia brassii *(Copel.) Parris* **comb. nov.**

Based on *Ctenopteris brassii* Copel., Univ. Calif. Publ. Bot. 18: 225 (1942). Type: New Guinea, *Brass* 9302 (holotype MICH 1115939!; isotypes A, BRI, K!, L 0051196!, PE!, UC!).

RANGE. New Guinea (West Papua, Papua New Guinea); endemic.

Prosaptia brassii has been treated as a synonym of *P. circumvallata* (Rosenst.) Copel. (Parris 1990), but the former has denser stipe and lamina hairs than the latter, and the abaxial surface of the rachis concolorous with the lamina rather than darker than it.

5. Prosaptia javanica *(Copel.) Parris* **comb. nov.**

Based on *Polypodium javanicum* Copel., Philipp. J. Sci., C. Bot. 8: 142 (1913). Type: Java, near Tjibodas, 1350-1850 m alt., *Owen Bryant Expedition* 298 (US!)

RANGE. Java; endemic.

Polypodium javanicum was regarded as a synonym of *Polypodium cryptosorum* C.Chr. (Backer & Posthumus 1931). The latter is a synonym of *Prosaptia barathrophylla* (Baker) M.G.Price, which has shorter darker frond hairs than *Prosaptia javanica*.

6. Prosaptia samoensis *(C.Chr.) Parris* **comb. nov.**

Based on *Polypodium emersonii* var. *samoense* C.Chr., B. P. Bishop Mus. Bull. 177: 111, t. 4c (1943). Type: Tau, trail to peak back of Tau, 430 m, 28 Jan. 1922, *D W Garber* 719 (lectotype BISH 105555 p. p.! largest plant, on left hand side, selected here; isolectotypes BISH 105555 p. p.! BISH 105560!). Residual syntypes: Samoa: Olosega, top of Piumafua, 630 m, *Garber* 1051 (BISH 105561!); Savaii, above Sili, 400 m, *Christophersen* 3178 (BISH 105558!); Ta'u, *Garber* 726 (BISH 105559!), *Garber* 731 (BISH 105554 p. p.!), *Garber* 747 (BISH 105617!); Tutuila, Alava Ridge, 400 m, *Christophersen* 1127 (BISH 105563!, UC!); top of Pioa, 500 m, *Christophersen* 1216 (BISH 105562!, UC!); Upolu, Malololelei-Lanutoo, 700 m, *Christophersen* 27 (BISH 105556!), *Christophersen* 35 (BISH 105565!); Vaisingano Canyon, 500 m,

Christophersen 78 (BISH 105557!, BM!, MICH 1190851!).
RANGE. Samoa (Olosega, Savaii, Ta'u, Tutuila, Upolu) and Tonga (Tafahi; *Buelow* 1178, 1230 (both CHR!)).
Christophersen 78 is the only syntype represented in Christensen's herbarium at BM and there is no indication of its type status on the specimen. The material chosen as lectotype is that illustrated when the variety was described.
Prosaptia samoensis differs from *P. alata* (Blume) Christ, of which *P. emersonii* (Hook. & Grev.) C.Presl is a synonym, in having denser short simple eglandular hairs on the sorus pouch, longer pinnae and a narrower wing along the rachis.

7. Stenogrammitis minutissima *(J.W.Moore) Parris* **comb. nov.**
Based on *Polypodium minutissimum* J.W.Moore, Bull. B. P. Bishop Mus. 102: 11 (1933).
Type: Society Is., Raiatea, Mount Temehani, E facing slope, 400 m alt., 7 Oct. 1926, *Moore* 187 (lectotype BISH 498922!, chosen here; isolectotype BISH 498923!).
RANGE. Society Islands (Raiatea); endemic to Mount Temehani and known only from the type collection.
Smith et al. (1991) did not include this species as a member of *Lellingeria*, nor did Labiak (2011) mention it when he separated *Stenogrammitis* from *Lellingeria*. *Stenogrammitis minutissima* differs from *S. subcoriacea* (Copel.) Labiak, also from the Society Islands (Tahiti) and in the Marquesas Islands, in the presence of forked hairs on the lamina margin, particularly at the apex of the pinnae, and on the abaxial surface of the rachis; no other types of hair are present. In *S. subcoriacea*, forked hairs, if present, are only at on the abaxial surface of the lamina near its base, and simple glandular and simple catenate hairs, if present, are only on the abaxial surface of the rachis.

8. Stenogrammitis subcoriacea *(Copel.) Labiak*
Syn. *Polypodium subcoriaceum* Copel., Bernice P. Bishop Mus. Bull. 93: 12 (1932).
Type: Society Islands, Tahiti, S. of Orohena, 1500 m, 16 May 1927, L. H. MacDaniels 1478.
Both Labiak (2011) and the TROPICOS on-line data base cite US material as the holotype and UC material as the isotype. The US collection is not the holotype, however. Copeland (1932) states in the introduction to his account of the pteridophytes of the Society Islands (where *Polypodium subcoriaceum* is described) that he identified material from the Bernice P. Bishop Museum (BISH) for this publication, so BISH is likely to have the holotype, not US. In BISH three sheets of MacDaniels 1478 were seen during a visit in 1992: BISH 500016, BISH 105458 and BISH 105459. In 2012 BISH 500016 and BISH 105458, but not BISH 105459, were seen again in BISH. As there is more than one sheet in BISH a lectotype needs to be chosen from the available material there. BISH 500016 barcode 1000428 bears the words "Polypodium subcoriaceum Copel. n. sp. TYPE" in Copeland's handwriting and is selected here as lectotype. BISH 105458 barcode 1000429 has a typed label, with "DUPL. TYPE" typed in the top right hand corner; this and BISH 105459, together with material in MICH!, UC! and US, are isolectotypes.

9. Tomophyllum duriusculum *(Christ) Parris* **comb. nov.**
Based on *Polypodium duriusculum* Christ, Verh. Natur. Gesell. Basle 11: 213 (1895).
Type: Celebes, G. Matinang N, c. 1000 m alt., 27 Aug. 1894, *Sarasin* 733 (P 00632869!).
RANGE. Sulawesi and Philippines (Luzon, *Barcelona* 541 *et al.* (PNH 190564!)).

10. Tomophyllum foersteri *(Rosenst.) Parris* **comb. nov.**
Based on *Polypodium bipinnatifidum* var. *foersteri* Rosenst., Repert. Spec. Nov. Regni Veg. 12: 179 (1913). Type: Nova Guinea germanica, Bolan Mts, 2400-3000 m alt., 1912, *Keysser* B 84 (S P7206!).
RANGE. New Guinea (West Papua, Papua New Guinea): endemic.
Tomophyllum foersteri was previously regarded as a variety of *T. bipinnatifidum* (Baker) Parris (Copeland 1953) or as a synonym of it (Parris 1990). The former differs from the latter, however, in having the rachis prominent and darker than the lamina on both surfaces and in having occasional to dense simple eglandular hairs on the abaxial surface of the lamina, including as receptacular paraphyses; the latter has the rachis prominent and concolorous on the abaxial surface and sunken and darker on the adaxial surface, with the abaxial surface of the lamina glabrous or rarely with occasional simple eglandular hairs that do not occur in the sorus as receptacular paraphyses.

11. Tomophyllum lividum *(Mett.) Parris* **comb. nov.**
Based on *Polypodium lividum* Mett., Ann. Mus. Lugd. Bat. 2: 221 (1866). Type: Java, *Korthals* s. n. (L!).
RANGE. Java; endemic.

12. Tomophyllum secundum *(Ridl.) Parris* **comb. nov.**
Based on *Polypodium secundum* Ridl., Trans. Linn. Soc. London, Bot. 2, 9: 262 (1916). Type: Dutch New Guinea, Mt Carstensz, Camps X to XI, 6700-8300 ft alt., *Boden Kloss* s. n. (lectotype BM 000800777!, chosen here). **Synonyms:** *P. subfalcatum* var. *semiintegrum* Copel., Philipp. J. Sci., C. Bot. 2: 138 (1907). *P. subsecundodissectum* var. *novoguineense* Rosenst., Nova Guinea 8: 725 (1912). Type: Nova Guinea neerlandica, summit of Hellwig Mts, 2583 m alt., Oct. 1909, *von Römer* 716 (lectotype L 913.103…129!, chosen here).
RANGE. Borneo (Sabah), Philippines (Mindoro), Moluccas (Seram), New Guinea (West Papua, Papua New Guinea).
Tomophyllum secundum was previously treated as a synonym of *T. subsecundodissectum* (Zoll.) Parris (Copeland 1953, Parris 2007), but the former differs in having all pinnae completely dimidiately lobed, or occasional pinnae in middle part of frond with a few basiscopic lobes in the apical part, while the latter has pinnae regularly with basiscopic lobes in the apical part.

13. Tomophyllum sesquipinnatum *(Copel.) Parris* **comb. nov.**
Based on *Ctenopteris sesquipinnata* Copel., Univ. Calif. Publ. Bot. 18: 225 (1942). Type: New Guinea, *Brass* 9510 (holotype MICH 1115918!; isotypes A, BRI, K 000491452!, L 0051190!, UC!).
RANGE. New Guinea (West Papua); endemic to Lake Habbema and known only from the type collection.
Tomophyllum sesquipinnatum was previously treated as a synonym of *T. bipinnatifidum* (Parris 2007), but the former differs from the latter in having a membranous, rather than a coriaceous lamina, and pinnae lobed less deeply, to a wing 0.3-0.5 mm wide along the costa rather than 0.1-0.3 mm wide.

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THE NOMENCLATURE, TYPIFICATION AND TAXONOMY OF *ASPLENIUM FALCATUM*, *A. POLYODON* AND CONFUSED SPECIES

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Key words: Pteridophytes, *Asplenium falcatum*, *Asplenium polyodon*, *Asplenium aethiopicum*, *Trichomanes adiantoides*, lectotype.

ABSTRACT

Asplenium falcatum Lam., described from Sri Lanka was a part of Linnaeus' concept of *Trichomanes adiantoides* L. The taxonomic history of *T. adiantoides* is outlined, showing that Linnaeus had a mixed concept and that the name had subsequently been taken in two different senses by later authors. It is lectotypified here in the sense of the African species known as *Asplenium aethiopicum* (Burm.f.) Bech. and a proposal to reject the name *T. adiantoides* and all combinations based on it is being prepared. This is intended to enable the Sri Lankan element within *T. adiantoides* to continue to be known by its well-known name, *A. falcatum* Lam., and the African as *A. aethiopicum*, which species are outlined further and their ranges in Africa and Asia are given. Although the name *A. polyodon* G.Forst. had recently been applied to *A. falcatum*, it is a distinct species confined to Australasia.

Other related S.E. Asian and Polynesian species are discussed briefly and contrasting diagnostic descriptions are provided to distinguish between the often confused species, *A. polyodon*, *A. falcatum* and *A. macrophyllum* Sw.

INTRODUCTION

A widespread and distinctive *Asplenium* species which occurs in Sri Lanka, South and N.E. India, S. China, S.E. Asia and Madagascar and the Mascarenes, had long been mentioned in Indian literature and elsewhere under the name *A. falcatum* Lam. But Morton (1967) concluded that the name *A. falcatum* was illegitimate due to the misapplication of the Linnaean name *Trichomanes adiantoides* L. by Lamarck, and took up the name *A. polyodon* G.Forst. to replace it.

Asplenium polyodon is a name that has been applied to a well-known species in Australasia and Oceania and was described from a plant that was most probably from New Zealand. It is superficially similar to the above *A. falcatum*, but after some years of doubt about the conspecificity of the Sri Lankan *etc.* plant and *A. polyodon*, we now report here that *A. polyodon* is a distinct species confined to Australasia and the Asian, *etc.* plant must therefore be known by another name. However, due to nomenclatural problems, it has not been clear by which name it should be known now that it is clear that *A. polyodon* is applicable to a different species.

Linnaeus (1753) created a considerable nomenclatural and taxonomic problem when he described *Trichomanes adiantoides* L., referring to previously published descriptions and illustrations by himself (Linnaeus, 1747), Burman (1737) and Plukenet (1691, 1696).

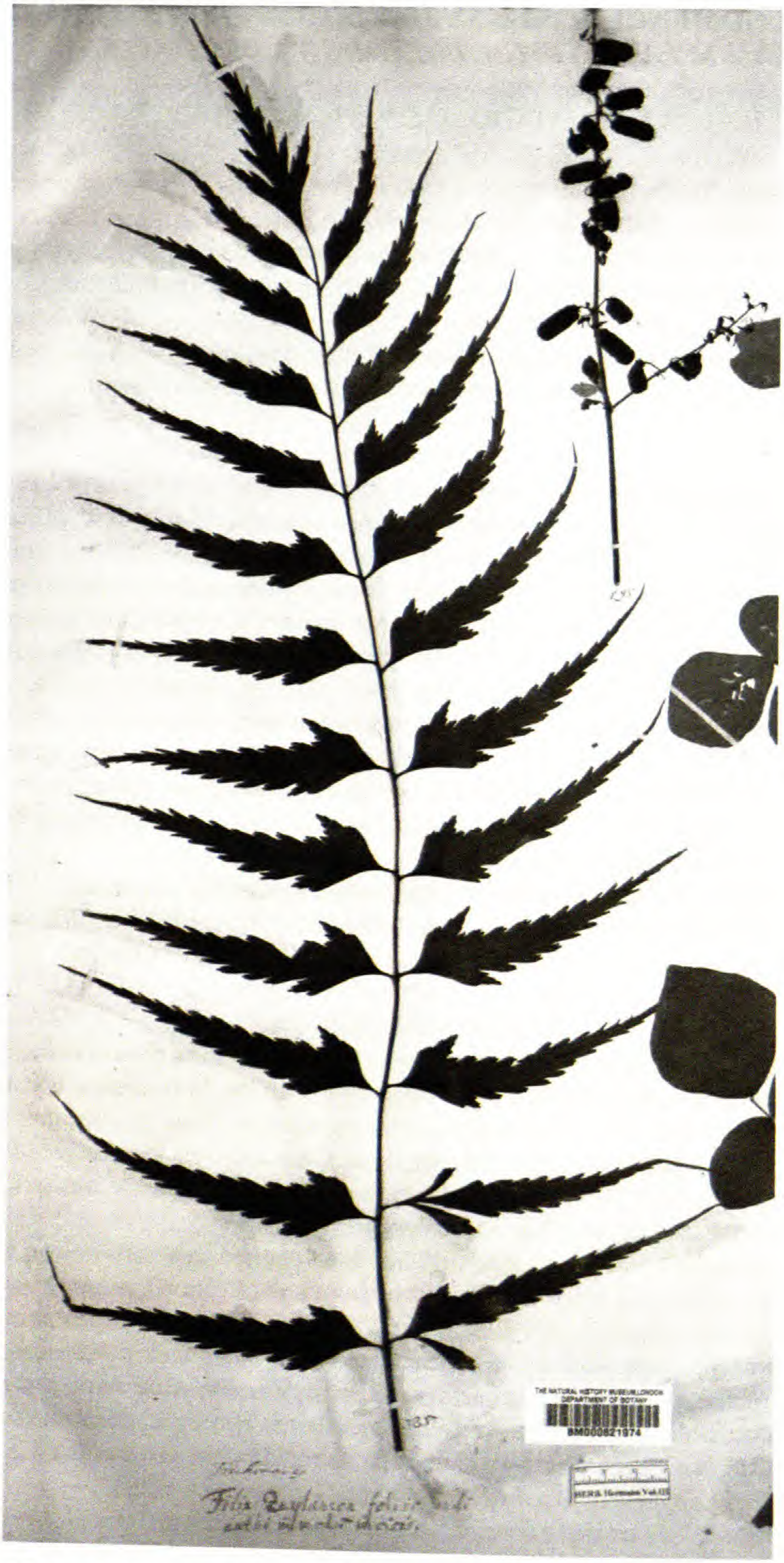

Figure 1. Hermann's fern. Herb. Hermann No. 385 (BM).

Burman's illustration was of a fern from Ceylon collected by Paulus Hermann, but Plukenet's plant was of a different species from Africa. The relevant plates show two very distinct ferns neither of which belongs in *Trichomanes* in its modern circumscription.

Hermann collected the plants in Sri Lanka and these are presently found in Leiden, in the Académie des Sciences (Institut de France, Paris) and the British Museum of Natural History. He gave a one-line description of a fern in his *Musaeum Zeylanicum* (1717) volume 3, fol. 47: "*Filix Zeylanica, foliis adianthi in modum incisis*" (Figure. 1). Johannes Burman (1737) published an illustration (Figure 2) of Hermann's fern, which is found at BM, and wrote a detailed description of the plant. He also added a reference to the African fern of Leonard Plukenet (1696), "*Adianthum africanum rutae murariae aemulum, segmentis longioribus acutis*", illustrated by Plukenet (1691) (Figure 3, 4). It was thus Burman who first made the incorrect connection between the African and Sri Lankan plants. Linnaeus maintained the confusion by including reference to both Burman and Plukenet under his *Trichomanes adiantoides* in *Flora Zeylanica* (1747: 35) and later in *Species Plantarum* (1753) and thus validated a name for a mixed concept based on two different species. Both voucher-specimens can be found in the historical collections at BM. Hermann's plant is in Herb. Hermann 3: 47, no. 385, and Plukenet's specimen is in Herb. Sloane 95: 16, at BM-SL (Figure 4). Burman's herbarium is in Geneva (G), but is not relevant to the case.

In his *Encyclopédie Méthodique*, Lamarck (1786) noticed the problem created by Burman and perpetuated by Linnaeus, and distinguished both species transferring both separately to the genus *Asplenium*, listing them under the French vernacular name for that genus, 'Doradille'. He remarked under '*Doradille adiantoïde*' that neither of the cited illustrations was of a *Trichomanes* but both were of true 'doradilles', and that the two species were quite different from each other. He treated the Sri Lankan species as *Asplenium falcatum* Lam., and the African fern as *Asplenium adiantoides* (L.) Lam. and noted that Linnaeus had included within *T. adiantoides* both the African plant illustrated by Plukenet and the Sri Lankan plant described by Burman. Hermann's words, "*Filix Zeylanica, foliis adianthi*" *etc.*, might appear to be related to the origin of the name *T. adiantoides*, but Linnaeus did not cite Hermann. He cited Burman (1737) and his own *Flora Zeylanica* (1747) both of which mention the African and the Sri Lankan plants. It could be argued that Lamarck should have applied the name *Asplenium adiantoides* to the Sri Lankan plant. On the other hand, it can be concluded that, as both the Burman and the Plukenet plants were mentioned by Linnaeus, either can have equal claim to his epithet *adiantoides*. Lamarck's choice was to apply the name *A. adiantoides* to the African element rather than the Sri Lankan.

Tardieu-Blot & Ching (1936) listed *A. adiantoides* Lam. as a synonym of *A. praemorsum* Sw., the name then being utilised instead of *A. aethiopicum*, and stated that Plukenet illustrated it for the first time but that Linnaeus had reported it in error under his *Trichomanes adiantoides*, which is a completely different plant. They also said that the type of *T. adiantoides* is a synonym of *Asplenium falcatum* Lam. and it can be found at Hermann's herbarium at Kew [*sic*] and it was well illustrated by Burman (1737). Following Christensen (1905) where he renamed the Sri Lankan plant *Asplenium adiantoides* - a later homonym of Lamarck's *A. adiantoides* - they concluded that the name *adiantoides* must be retained for the Sri Lankan plant - the *Asplenium falcatum* of Lamarck - which they called "la plante de Linné", the Linnaean plant, while *A. adiantoides* Lam. must be called *A. praemorsum*, the African plant. While this is one

possible interpretation, it is also entirely arbitrary and went against Lamarck's conclusion. As they stated that the type is the specimen in Hermann's herbarium (actually at BM, not Kew), this cannot be taken as valid lectotypification as the type has to be the illustration Linnaeus cited.

Figure 2. Type plate Burman t. 43 cited by Linnaeus under *Trichomanes adiantoides* in *Flora Zeylanica* (1748) and *Species Plantarum* (1753). This plant is from Ceylon and was renamed *Asplenium falcatum* by Lamarck.

Morton (1967) similarly was of the clear, if arbitrary opinion that the Sri Lankan plant should have been the element identified as *Trichomanes adiantoides*. According to him, since Burman had begun his brief description by stating that this fern was "*Filix non ramosa Zeylanica...*" and then mentioned its leaves as being serrate in the way of an *Adiantum*, he reasoned that Linnaeus' main intention must therefore have been to use the Ceylon plant as the basis for *T. adiantoides*. He went so far as to say that the type of *A. adiantoides* "must be the Ceylon plant", though without formally selecting a type. He therefore concluded that de Lamarck should not have applied the name *A. adiantoides* to the African plant, though in reality he was free to do so.

Two pieces of evidence linking Linnaeus' account to Hermann's specimen (Figure 1) are shown by the citation in *Flora Zeylanica* of what was actually Linnaeus' number 385, and by the name *Trichomanes,* which was written in Linnaeus' own handwriting on Hermann's original specimen. Linnaeus cited his *Flora Zeylanica* account of *Trichomanes adiantoides* in *Species Plantarum*, and this account was based on the Hermann specimen that he unambiguously annotated, though he did not make direct reference to the specimen in *Flora Zeylanica* or *Species Plantarum*. The Hermann material at BM is original and should be considered for lectotypification purposes. Therefore, the type specimen of *Trichomanes adiantoides* must be chosen from either the Hermann specimen (Herb. Hermann 3: 47, no. 385 at BM), Plukenet specimen (Herb. Sloane 95: 16, at BM-SL) or either of the illustrations mentioned by Linnaeus in his *Species Plantarum*.

According to Morton's interpretation of *T. adiantoides*, when Lamarck named the Sri Lankan plant *A. falcatum* Lam., that name was a *nomen novum* for *T. adiantoides* and not a new species, since the Sri Lankan plant was in his view the basis and type of *T. adiantoides*. He therefore treated *A. falcatum* as an illegitimate *nomen superfluum*. Furthermore he concluded that Lamarck's *Asplenium adiantoides* from Africa, a synonym of *A. aethiopicum* (Burm.f.) Bech., was not a new combination, as would appear to be the case, but was independent of *Trichomanes adiantoides* L. (from Sri Lanka), despite Lamarck's citation of it. Morton concluded, "*Lamarck was therefore unjustified in typifying the Linnaean species on the basis of the African plant illustrated by Plukenet.*"

One subsequent statement on typification was made by Brownsey (1998), who under *T. adiantoides* L. in the synonymy of *A. polyodon*, cited: "T: Ceylon [Sri Lanka]; holo: BM (Herb. Burman 385)." At first sight this appears to constitute lectotypification despite the statement in the introduction that "*these type statements are not to be interpreted as lectotypifications*", because it also says that the type citations under taxa "*reflect the authors' belief in their current status*" and under the Code (McNeill, 2012: Art 9.9), the use of a wrong term for a type is merely treated as an error to be corrected (in this case holotype instead of lectotype). The process of lectotypification under the ICBN does not allow for disavowal of intent. However, Herb. Burman is in G, not BM as cited (it should have been Herb. Hermann) and there is no such specimen as Burman no. 385, which was the reference given in Linnaeus' *Flora Zeylanica* to Hermann's specimen no. 385. Thus this statement cannot be taken as lectotypification as no actual existing element was cited, nor the correct herbarium.

Lectotypification of *Trichomanes adiantoides* L.

Lamarck was correct in separating the two species, but the present difficulty concerning the correct application of names is due to subsequent disagreement about his application of the epithet *adiantoides* and his choice to name the Sri Lankan plant independently.

Figure 3. Plukenet's illustration cited by Burman (1737) and Linnaeus (1753).

Linnaeus' simple diagnosis fits either the Sri Lankan or the African fern almost equally, either of which can therefore be chosen as lectotype. Thus, in contrast to Morton's argument, it can be concluded alternatively that the name *A. falcatum* Lam. is legitimate as a new Sri Lankan species, when the name *A. adiantoides* (L.) Lam., understood as being a new combination based on Linnaeus' name, is applied to the African species, as Lamarck did.

There also remains the question of the typification of *T. adiantoides* because neither Linnaeus, Lamarck, Christensen, Tardieu-Blot & Ching, nor Morton selected a single element that can nowadays be taken as being a lectotype. As pointed out to C.R. Fraser-Jenkins by C.E. Jarvis (*in litt.* 26 Oct. 2005), though they made reference to various descriptions and illustrations, they either chose a specimen incorrectly or did not unequivocally select a single element as type, this was therefore insufficient to be taken as modern lectotypification.

It has now become essential to select between either the Sri Lankan element or the African element as a permanent lectotype of *T. adiantoides* in order to elucidate the nomenclature definitively. As discussed above, there are two options for the choice, both being consistent with Linnaeus' protologue and both being tenable.

The nomenclatural consequences of the two possible options for lectotypification are as follows:

1. Lectotypification of *T. adiantoides* based on the Sri Lankan element (following Morton):

a. *Trichomanes adiantoides* L., *non A. adiantoides* Lam., becomes a synonym of *Asplenium* sp. from Sri Lanka and S. India, *etc.* The epithet *adiantoides* cannot be used for the Sri Lankan species, as the combination is preoccupied in *Asplenium* by *A. adiantoides* Lam, the African species.

b. *Asplenium adiantoides* Lam., the African species, becomes a synonym of *A. aethiopicum* (Burm.f) Bech. The African plant remains *A. aethiopicum*, which name was first applied to it by Becherer (1936) in lieu of *A. praemorsum*.

c. *Asplenium falcatum* Lam. becomes an illegitimate name as Lamarck cited *T. adiantoides* in its synonymy so it is a *nom. nov.* for *T. adiantoides* as he should have chosen the epithet *adiantoides* instead, which was available.

d. The Sri Lankan and South Indian plant would need to be known by a different name from either *A. falcatum* or *A. polyodon*, but it is unclear whether another name exists or whether it would have to be described as a new species due to the existence in literature of several related but obscure names, no longer in use, from different parts of Africa and Asia.

e. Providing a name for Linnaeus' Sri Lankan plant is therefore very difficult and would require years of further investigate research in two continents and several different regions.

2. Lectotypification of *T. adiantoides* L. based on the African plant (following Lamarck):

a. *Asplenium adiantoides* (L.) Lam. becomes the correct name for *A. aethiopicum* and the

type is not Lamarck's African specimen collected by Sonnerat (Figure 4), but the Plukenet illustration cited by Linnaeus (Figure 3).

b. *Asplenium falcatum* Lam., as an independent new species, is no longer superfluous and illegitimate, and becomes the correct name for the Sri Lankan and S. Indian plant.

c. The undesirability of a name-change for the very widely known and widespread Asian and African species, *A. aethiopicum* (to *A. adiantoides*), can be solved by a proposal to reject the name *T. adiantoides*.

d. In the unlikely event that this proposal were to be rejected, a name-change for *A. aethiopicum* would result. But if it was accepted, nomenclatural stability will have been achieved as the well-known names, *A. falcatum* and *A. aethiopicum*, will apply to the two species.

We believe that in the interests of nomenclatural stability and given the equal claim of each option, we should follow Lamarck's choice, which is to typify *T. adiantoides* in the sense of African plant, and at the same time to submit a formal proposal (Fraser-Jenkins

Figure 4. Plukenet's specimen. Herb. Sloane (BM-SL 96:16).

et al., in prep.) for the rejection of the name *T. adiantoides* and all combinations based upon it. This will enable the African/S. Asian plant to continue to be known as *A. aethiopicum* and the Sri Lankan/Indian plant to continue to be called *A. falcatum*. Accordingly we now select as lectotype, here designated, of *Trichomanes adiantoides* L., *Sp. Pl.*. **2**:1098 (1753), the following illustration, Plukenet, Phytographia 3: t. 123. f. 6 (1691; Figure 3). We also select an epitype, here designated, to assist in the precise and critical identification of the above lectotype, "South Africa, Cape Province, Kalk Bay Mountain, in rock crevices, *c.* 1000 ft. *A.F. Braithwaite 75*, 25 Aug. 1960 (K)", octaploid sexual, det. A.F. Braithwaite (1986).

Figure 5. *Asplenium aethiopicum* (Burm.f.) Bech., *Sonnerat s.n.* (Herb. Lamarck, P).

Lectotypification of *Asplenium falcatum* Lam.

The Sri Lankan *etc*. plant Linnaeus was referring to is now once more to be called *A. falcatum* Lam., as it used to be widely known previously. Lamarck, however, did not

Figure 6. *Asplenium falcatum* Lam., *Sledge 873* (epitype, BM).

specify the type of *Asplenium falcatum*, though he applied the name to Linnaeus' Sri Lankan element. We therefore select as lectotype, here designated, of *A. falcatum* Lam., *Encycl. Méth. Bot.* **2**(1): 306 (1786), the illustration in Burman's *Thesaurus Zeylanicus*, t. 43 (1737). Burman wrote a detailed description of this plant published together with the plate (Figure 2). This illustration is a very good and accurate representation of the Hermann specimen in Herb. Hermann 3: 47 (Figure 1, BM) and most usefully shows the long sori on the underside, though the specimen is now pasted down to show only the top surface. Linnaeus cited this reference, among others, under *Trichomanes adiantoides* in *Flora Zeylanica* (1747) and *Species Plantarum* (1753). The plant is from Sri Lanka and was renamed *Asplenium falcatum* by Lamarck. In order to help with identification, we here designate as epitype of the above lectotype: "Ceylon, in forest in the upper part of Ritigala, N. Cent. Province, alt. 2250 ft., *W. A. Sledge* 873, 14 Jan. 1951 (BM)" (cited by Sledge 1965; Fig 6). Similar material from Sri Lanka was found by Manton & Sledge (1954) to be octaploid sexual, but we are as yet unable to find their Sri Lankan voucher-specimen, which should be among their extensive unincorporated material at BM. *Asplenium falcatum* is not conspecific with the Australasian species, *A. polyodon* G.Forst., which Morton confused it with (though, as he stated, taken in a broad sense). Pending rejection of *T. adiantoides* L., *nomina ubique rejic. prop.*, the African (and S. Asian) plant referred to by Linnaeus should continue to be called *A. aethiopicum* (Burm.f.) Bech. subsp. *aethiopicum* (see below re subspecies), with *T. adiantoides* L. and *A. adiantoides* (L.) Lam. in its synonymy.

Taxonomic comments on species

Asplenium aethiopicum (Burm.f.) Bech.

Lamarck also mentioned two further specimens of *A. adiantoides*, one collected in Africa by Sonnerat (Figure 5) but without specific locality, and the other in Mauritius by Commerson (Figure 7). Both specimens are preserved in Herb. Lamarck at P. The Sonnerat specimen bears Lamarck's annotation "*vide Pluk. Fig. 123, t.6*" and belongs to *A. aethiopicum*, while the Commerson specimen was a misidentification by Lamarck as it belongs to *A. falcatum*. However neither plant cited by Lamarck has type status as they were not included by Linnaeus as part of his concept.

Morton (1967), followed by Schelpe & Anthony (1986), designated the Commerson specimen as lectotype of *A. adiantoides* Lam. (Figure 7), but taking the name as if independent from Linnaeus' name. This lectotypification therefore does not stand as it was not one of the elements cited by Linnaeus.

Christensen (1905) again made the combination *A. adiantoides* (L.) C.Chr., as if independent of Lamarck's name, which latter he listed separately and identified as being *A. praemorsum* Sw. taken in a wide sense, meaning *A. aethiopicum* (as at that time no-one knew the identity of *Trichomanes aethiopicum* Burm.f.). But his new combination was mistaken as it was an illegitimate later homonym of Lamarck's and had also been utilised independently in the meantime by Raddi (1819) and Raoul (1844). He took the Linnaean basionym and his attempted combination in the sense of the Sri Lankan plant, placing *A. falcatum* Lam. in its synonymy.

By the time Lamarck mentioned the African plant, it had already been described and named three times. The oldest description was by Nicolaas Burman (1768) under the name *Trichomanes aethiopicum* Burm.f. Becherer (1936) transferred this to *Asplenium* and the species is now known as *Asplenium aethiopicum* (Burm.f.) Bech. This is a widespread, phenotypically and cytologically variable subtropical species found

Figure 7. *Asplenium falcatum* Lam., Île de France (Mauritius), *Commerson s.n.*, (Herb. Lamarck, sheet 1, not a type, P).

throughout Africa, the Mascarenes, Macaronesia, S.E. and South Asia (including Myanmar, Thailand, China, Vietnam, Sri Lanka, S. India, and in one locality in N.E. India), with the closely related species or subspecies, *A. praemorsum* Sw., occurring in C. and S. America. In Africa it is a member of a highly critical allopolyploid pillar complex, whose members have frequently been confused with each other, but nevertheless usually have distinct frond-morphology. The subspecies of the complex were elucidated and delineated morphologically and cytologically by Braithwaite (1984, 1986) and are now well established in African, European and Asian literature. *Asplenium aethiopicum* is typified by a specimen from the Cape of Good Hope, in Herb. Burman (G). It is known to be an octaploid sexual taxon, subsp. *aethiopicum*; exactly the same taxon also occurs commonly, and has been confirmed through chromosome counts, in South India and Sri Lanka, and the same subspecies has probably been discovered recently in Assam, N.E. India, as well (Odyuo *et al.* 2012).

As stated above, *T. adiantoides* L. and *A. adiantoides* (L.) Lam. are being proposed as *nomina ubique rejic. prop.* and will thus be synonyms of *A. aethiopicum* if the proposal is accepted.

The detailed range of *A. aethiopicum* is Macaronesia (Madeira, cytologically distinct), West, South and throughout East Africa, the Comoros, Madagascar, Mauritius, La Réunion, Yemen, South and N.E. India (Andamans, Tamil Nadu, Kerala, Karnataka, Andhra Pradesh, Assam), Sri Lanka, Myanmar, Thailand, Vietnam, S. and S.W. China, Malaysia, Java, the Philippines, Australia, New Caledonia, Oceania. Records from Hawai'i and C. and S. America refer to the closely related *A. praemorsum* Sw., which is probably best treated as a further subspecies of *A. aethiopicum*, and which is generally rather less lobed in its pinnae.

It should be noted that whereas in much recent Indian literature following Morton (1973), the name *A. gueinzianum* Mett. *ex* Kuhn, described from Natal, is applied to what used to be known in North India and China as *A. laciniatum sensu* Hook., *non* D.Don, the latter species is not known from Africa and Morton misidentified *A. guienzianum*. Although Morton thought the type of *A. gueinzianum* looked indistinguishable from the Indian plant, Schelpe & Anthony (1986) also saw the type and placed it within *A. aethiopicum*, but it has subsequently been precisely identified by Roux (2009) as being conspecific with the purely African species, *A. friesiorum* C.Chr., whose name it therefore replaces. Recent unresearched misapplication of the name *A. gueinzianum* in India and China is entirely erroneous. Fraser-Jenkins *et al.* (2011) renamed the Indian and Chinese plant as *A. lacinioides* Fraser-Jenk., which has been overlooked among a number of other taxonomic and nomenclatural errors in the genus in the *Flora of China* (2013).

Asplenium falcatum Lam.

Until the time of Morton's (1967) publication, the name *A. falcatum* was widely used for plants from Africa, India (partly in error for the species known there as "*A. macrophyllum*" *auct.*, *non* Sw. and for *A. finlaysonianum* Wall. *ex* Hook. in N.E. India), Sri Lanka, S.E. Asia and China to Polynesia (the latter in error for related species). Several of these plants are not conspecific with *A. falcatum*, though of the same general habit. But following Morton (1967) in believing that *A. falcatum* was an illegitimate superfluous name, botanists did not hesitate to use the name *A. polyodon*, newly proposed as applying to the plants previously named as *A. falcatum*; see for example Sledge (1982), who had previously utilised the name *A. falcatum* (Sledge, 1965) from Sri Lanka. In South India and mainland China, however, Morton's publications remained almost

Figure 8. *Asplenium polyodon* G.Forst., ., "Insulae Oceani Pacifici", *G. Forster s.n* (lectotype,UPS).

unknown and use of the name *A. falcatum* persisted until recently. It was still used by Wu (1999) in the *Flora Reipublicae Popularis Sinicae*, with *A. polyodon* given in synonymy, but without being aware of the complications, while the *Flora of China* (2013) simply followed Morton without necessary research and misapplied the name *A. polyodon* to it. Otherwise the name *A. falcatum* has practically disappeared from new collections in many herbaria, which have instead adopted *A. polyodon* as if the correct name. But as mentioned above, the two are different species and *A. falcatum* is now restored as the correct name for the Sri Lankan and Indian *etc*. plant. *A. falcatum* has been found to be a sexual tetraploid species in Sri Lanka (Manton & Sledge, 1954) and N. India (Bir 1960), both voucher-specimens checked and confirmed by CRFJ, though other records from India are unreliable and without voucher-specimens. Various reports from other countries *sub A. polyodon* do not refer to *A. falcatum*.

The detailed range of *A. falcatum* as construed here is Madagascar, the Mascarenes (Mauritius, La Réunion, Rodriguez), S., C. and N.E. India (Andamans, Nicobars, Tamil Nadu, Kerala, Karnataka, Orissa, W. Bengal (Teesta - Siliguri), Assam, Nagaland, Arunachal Pradesh), ?Bangladesh, Sri Lanka, across mainland S. China (Yunnan to Hainan), Taiwan, Myanmar, Thailand, Vietnam, Malaysia and Indonesia to the Philippines. Reports from N.E. India are mainly in error for "*A. macrophyllum*" *sensu auct. Ind.*, *non* Sw. (see below), or sometimes for *A. finlaysonianum* Wall. *ex* Hook., or *A. khasianum* Sledge, but *A. falcatum* also occurs there as a rarity. A more deeply lobed or pinnatifidly pinnate plant from S. India, Sri Lanka and Malaya is *A. mysorense* Roth (syn. *A. falcatum* var. *bipinnatum* (Sledge) Sledge; *A. bipinnatum* (Sledge) Philcox, *non* C.Chr.). But the plants from Australasia are *A. polyodon* (see below), which does not occur in India or Africa, despite reports in error for *A. falcatum*. *Asplenium falcatum* can also be confused with the S. Indian and Sri Lankan species, *A. decrescens* Kunze, especially when the pinnae of *A. falcatum* are narrower than usual, as often occurs as part of its individual variation. But *A. decrescens* has a long-creeping rhizome and apart from in the basal acroscopic lobe, the sori are parallel to and almost confined to a line along the midrib of the pinna, and do not point directly outwards nearly to the margin. None of these species occurs in the C. or W. Indo-Himalaya, as sometimes reported in error.

Polynesian plants previously reported as *A. falcatum* may represent one or more distinct species, and require further study.

Asplenium polyodon G.Forst. (*non* Wall. *nom. nud.*).

Georg Forster described *A. polyodon* from a plant he probably collected in New Zealand during Captain James Cook's second trip to the Pacific (Figure 8). The species was described in his Australian *Prodromus* (1786), the same year as *A. falcatum* Lam., together with many other new species collected during the voyage of H.M.S. *Challenger*. Unfortunately Forster did not specify anything that could now be taken as a holotype, nor gave the locality, and apparently the only surviving specimen of *A. polyodon* collected by him is a small, sterile, juvenile frond found in the Thunberg Herbarium in Uppsala, UPS (Figure 8). Nicolson & Fosberg (2004) designated this specimen as the lectotype of *A. polyodon*. Hooker (1860) considered *A. polyodon* identical to *A. falcatum* Lam. and commented on the variability of the latter species and that under his rather wider species concepts it intergrades imperceptibly into *A. macrophyllum* Sw., *A. caudatum* G.Forst. and others. Christensen (1905) listed *A. polyodon* as both a synonym and a variety of his sense of *A. adiantoides*. However we now report from study of and familiarity with the

Australasian plant, that this species differs from *A. falcatum* Lam. in its more scaly stipe and rachis, more lobed pinnae, shape of the apical segment and in its sori, as well as in its geographical distribution (Figs. 9, 10, 11, 12, 13, 14). The two are clearly not conspecific, which was perhaps slightly reflected by Christensen's mentioning it as a variety and Morton's stating, "in a broad sense", which latter comment was unfortunately overlooked by recent authors.

The name *A. polyodon* G.Forst. should be restricted to plants from New Zealand, Australia and adjacent islands including New Caledonia. Some plants from Australia, Norfolk Island and Lord Howe Island differ from those in New Zealand in having long, acuminate pinnae, the margin incised with blunt teeth, a single row of parallel to diverging sori ending at a distance from the margin, and the lowest pinna-pairs often not being reduced in size. The taxonomic status of these plants requires further study. New

Figure 9. *Asplenium falcatum* Lam. Pinna shape, serration and soral arrangement. *Commerson s.n.* (Herb. Lamarck, sheet 1, not a type, P).

Caledonia has other closely related plants that may represent at least two perhaps infraspecific taxa, and one new species with a creeping rhizome. Despite previous reports, true *A. polyodon* also does not occur in Polynesia, where different species appear to replace it.

Wallich (1828: 63) mentioned *Asplenium polyodon* Wall. (*nom. nud.*) as the name for what he had previously called *Asplenium porrectum* Wall. (*Num. List* no. 224), from Mauritius, which was equated by Christensen (1905) with *A. protensum* Schrad. It is independent of *A. polyodon* G.Forst.

Asplenium macrophyllum Sw.

Aspelnium macrophyllum Sw. (1801) is much closer to *A. falcatum* and belongs to the same group. In a broad sense, it would probably have been a better choice than *A.*

Figure 10. *Asplenium polyodon* G.Forst. Pinna shape, serration and soral arrangement. *R. Schodde* 316 (BM).

polyodon to replace the supposedly illegitimate name *A. falcatum* and some previous taxonomists had even considered it a large form of *A. falcatum*. But it is clearly a distinct species. It is based on a plant collected by Groendal in Mauritius (Figure 15), of which the holotype is a rather poor specimen, preserved in S. *Asplenium macrophyllum* differs from *A. falcatum* in having fewer pinnae, which are wider, and more ovate at their bases, with longer, less prominently serrate and straight apices, sometimes with long-acute subapical lobes and ending in a long-acute or short acuminate tip. The stipe is also less scaly. *Asplenium macrophyllum* does not agree with Hermann's specimen and Burman's illustration. It is certainly known only from the Mascarenes, though it has often been

Figure 11. *Asplenium falcatum* Lam. apical segment. *Commerson s. n.* (P).

reported from N.E. India (W. Bengal, Darjeeling Distr.; south Sikkim; and Assam (from where it has been confirmed cytologically as a sexual tetraploid)), Bangladesh, Myanmar, Thailand, through South-East Asia and Borneo to the Philippines.

At least the Indian subcontinental plant, also including Myanmar and Thailand, is not the same as true *A. macrophyllum* from the Mascarenes and appears to represent a distinct species, closer to, but distinct from *A. falcatum*. This currently unidentified species does not have the ovate pinna-bases of *A. macrophyllum*, and also has fewer pinnae, with fewer lobes and less teeth than in *A. falcatum*. It is currently under study by the present authors in comparison with S.E. Asian species. It is an uncommon fern, poorly represented in herbaria and in the past has sometimes been confused with *A. finlaysonianum* Wall. *ex* Hook. (*e.g.* from Nepal).

Figure 12. *Asplenium polyodon* G.Forst. Apical segment shape and pinna serration. Mere Mere Rd., Hawera, North Island, New Zealand. *Linsaght 1* (BM).

Figure 13. *Asplenium falcatum* Lam. Lowest pinnae not decreasing. , Île de France (Mauritius *Commerson s.n.*, (Herb. Lamarck, not a type, sheet 2, P).

Asplenium macrophyllum is absent from Polynesia and Australasia and reports from the former refer to apparently different taxa.

Asplenium cultratum Gaudich.

Gaudichaud-Beaupré (1828) described *Asplenium cultratum* Gaudich. from a plant collected in Guam, Marianas, during the voyage of Captain Freycinet around the world, the type being at P (Figure 16). Considered for a long time to be a synonym of *A. falcatum* Lam., this is the next oldest name without previous homonyms that would have been a possible replacement for it, if applied in a broad sense. But the type and other collections of *A. cultratum* do not quite match the Hermann specimen or other collections from Sri Lanka very well and might perhaps represent a distinct species. Particularly for this reason it is fortunate that there does not have to be a replacement for the name *A. falcatum*.

Asplenium urophyllum Wall. *nom. nud.*

Asplenium urophyllum Wall. is another name that has occasionally been used for plants of *A. falcatum* that are more deeply serrate. Otherwise, it is practically indistinguishable from *A. falcatum*. It was a *nomen nudum* mentioned by Wallich (1828) in his *Numerical List* or *Catalogue* as collected from Penang, Malaya, by George Porter. It has occasionally been listed as *A. macrophyllum* var. *urophyllum* Hooker (1860), who validated the name at varietal rank. Christensen (1905) listed it as a synonym of either *A. adiantoides* (L.) C.Chr. or *A. macrophyllum* Swartz. It seems likely that it is only a more serrate-lobed stage or form of *A. falcatum*.

Polynesian species related to *A. falcatum* and *A. polyodon*

Polynesian plants have traditionally been identified as *A. polyodon*, *A. macrophyllum* or *A. falcatum*, depending on the period when the specimens' identity was determined by botanists. True *A. polyodon*, *A. macrophyllum* and *A. falcatum* do not occur in the Marianas, Fiji, Tonga, Samoa or other Polynesian islands further east. The Polynesian plants differ in details of the frond apical segment, pinna margin and shape, and sori. The paucity of samples from the major groups of Polynesian islands in European herbaria makes it difficult to determine the ranges of variation that may exist. This species-complex clearly requires further study in Polynesia as the species have not been fully elucidated there.

Diagnostic comparisons of *A. falcatum*, *A. macrophyllum* and *A. polyodon*

1. Rachis scales narrow and ribbon-like or folded forming a concave cavity at the base of the scale, with 2-4 narrow branches along the margin. Lowest pinna pairs reducing; frond apical segment different from pinnae, narrow, pinnatifid and incised, base narrow and unevenly cuneate, formed by two adnate pinnae, margin incised and serrate, two rows of sori, one parallel to the rachis; pinnae narrowly trapeziform, base unevenly cuneate; pinna margin incised, forming serrate lobes; veins oblique to the costa, forking two or three times; sori very prominent, forming two rows, first row parallel then diverging from the costa, second row of sori after the second fork, never reaching near to the margin; sori 16 – 20 cm long .....***A. polyodon***
(Figs. 10, 12, 14)

2. Rachis scales wide and flat, not forming a concave cavity at the base of the scale, with

3-6 short branches around the base. Lowest pinna pairs of the same length as middle pinnae; frond apical segment wide to very wide, ovate-lanceolate, base broadly and evenly cuneate, margin finely serrate throughout, often with two long acuminate basal lobes resembling attached pinna-like lobes, with all sori in a single row at an oblique angle to the costa; pinnae wide, ovate-trapeziform, base unevenly cuneate; veins oblique

Figure 14. *Asplenium polyodon* G.Forst. Lowest pinna pair reducing. *R. Schodde* 316 (BM).

to the costa, forking usually once or twice into two long veinlets; sori not prominent, in a single row, always oblique to the costa, very long extending from near the costa to near the margin; sori up to 30 cm long.....3a.

Pinnae many, elongated trapeziform (1.0-)1.76-2.6(-2.76) cm wide, (6-)7-11(-16) cm long, 4-6 times longer than wider, falcate, pinna apex long acuminate, pinna margin unevenly serrate near the base, evenly serrate near apex.....***A. falcatum*** (Figure 7, 9, 11, 13)

Figure 15. *Asplenium macrophyllum* Sw., *Groendal s.n.*, Mauritius (type, S).

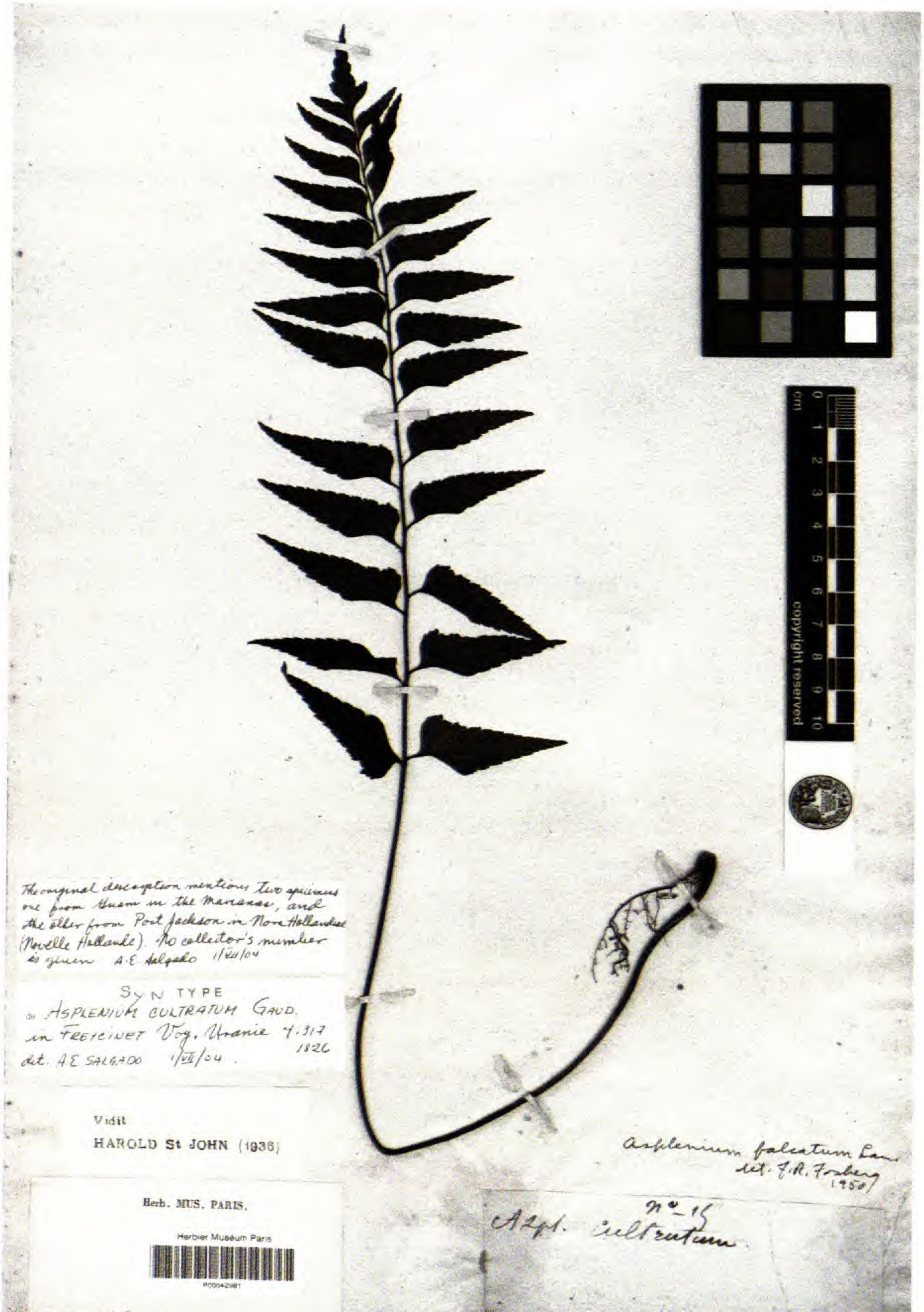

Figure 16. *Asplenium cultratum* Gaudich., Syntype: *Gaudichaud s.n.*, Guam, Marianas Is. (with permission, courtesy Herb. P.)

3b. Pinnae few, trapeziform (2.6-)3-6(-7) cm wide, 10-18(-20) cm long, 2-3 times longer than wide, straight, pinna apex acute to shortly acuminate, pinna margin notched to unevenly serrate throughout the length of the pinna .....***A. macrophyllum*** (Figure 15)

CONCLUSIONS

1. *Trichomanes adiantoides* L. is lectotypified by Linnaeus' African plant, now called *A. aethiopicum* (Burm.f.) Bech. *Trichomanes adiantoides* and all combinations based upon it are soon to be proposed as *nom. ubique rejic. prop.*
2. *Asplenium falcatum* Lam. is a legitimate name described from Sri Lanka and should be used.
3. *Asplenium polyodon* G.Forst. is specifically distinct from *A. falcatum* Lam. This name should only be applied to plants from Australia, New Zealand and adjacent islands.
4. *Asplenium macrophyllum* Sw. is specifically distinct from *A. falcatum* Lam. (and *A. polyodon* G.Forst.) and occurs in the Mascarenes. The name should not be applied to *A. falcatum*, nor to the unnamed species reported as "*A. macrophyllum*" from India *etc.*
5. Plukenet's African fern (also in S. Asia, *etc.*) should continue to be known as *Asplenium aethiopicum* (Burm.f) Bech. subsp. *aethiopicum* in anticipation of the rejection of *T. adiantoides* L. and *A. adiantoides* (L.) Lam.
6. Polynesian plants are different from the typical *A. polyodon* G.Forst. and *A. falcatum* Lam. and require further study.

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